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The Structure and Evolution of Teeth in Lungfishes

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INTRODUCTION

The most distinctive characteristics of Dipnoi, present even in the earliest known members of the group, are modifications of the skull and jaws that are related presumably to a particular manner of feeding. The cranium is solidly constructed with a completely fused, holostylic jaw suspension. The lower jaws are short and articulate far forward, resulting in a small gape and a powerful bite. The marginal jaw bones and teeth are reduced or lost, and paired tooth plates with radiating ridges and grooves are commonly developed on the pterygoids and prearticulars. All of these characters are clearly related to an adaptation for powerful jaw action, often for crushing food, though not necessarily hard food as is sometimes assumed. The ridged tooth plates have been considered an essential part of this adaptation, and as such, a part of the original set of characters that differentiated Dipnoi from their crossopterygian relatives at the start of their evolutionary history. As a necessary consequence of this theory, lungfishes that lacked tooth plates would have been derived from ancestors that possessed them. In the cases of *Conchopoma* and *Uronemus*, Watson and Gill (1923, p. 214) thought that this may have resulted neotenically by carrying larval denticles into adult life. Lehman (1959, p. 34) attributed the isolated denticles of *Soederberghia* to the same cause, and Graham-Smith and Westoll (1937, pp. 258-259) considered this possible in *Fleurantia*. This theory is acceptable on purely morphological grounds, but the chronological occurrence of early lungfishes furnishes strong reasons to question it. Thus, during the Devonian period, though approximately half

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of the genera possessed tooth plates, still at least one-third did not; this is illustrated by the list below:

Dental plates present	Dental plates absent	Teeth unknown
Chirodipterus	[1]*Dipnorhynchus lehmanni*	*Jarvikia*
Conchodus	[1]*Dipnorhynchus sussmilchi*	*Melanognathus*
Dipterus	*Fleurantia*	*Nielsenia*
Grossipterus	[2]*Ganorhynchus splendens*	*Rhynchodipterus*
Oervigia	*Griphognathus*	
Palaedaphus	*Holodipterus*	
? *Pentlandia*	*Soederberghia*	
Phaneropleuron	*Uranolophus*	
Rhinodipterus		
Scaumenacia		
Sunwapta		

In the late Paleozoic, dental plates are present in six genera *(Ctenodus, Gnathorhiza, Monongahela, Proceratodus, Sagenodus,* and *Tranodis),* absent in two *(Conchopoma* and *Uronemus),* and uncertain in one *(Straitonia).* Probably all post-Paleozoic Dipnoi had tooth plates.

This record suggests that in early dipnoan history there was considerable experimentation with dental apparatuses, rather than stabilization on a single type. This is reasonable because experience has shown that experimentation is common during the early history of many groups. It avoids the rather unlikely derivation of "plateless" genera from those with dental plates, and it indicates that dental plates can no longer be considered as typical of Dipnoi, though they are by far their most successful dental adaptation. It also must be taken into account in classification, for it means that "plateless" genera are not necessarily derived from nor closely related to those with dental plates.

This study does not purport to be a complete survey of lungfish teeth, but is based largely on the literature and on specimens in Field Museum of Natural History. All specimen and thin-section numbers are those of the Geology Department in that institution, unless otherwise specified. I wish to express my gratitude to Dr. Roger S. Miles for the loan for sectioning of specimens of *Dipterus valenciennesi* in the Royal Scottish Museum. The Australian National University through Dr. K. S. W. Campbell kindly presented a cast of the skull of *Dipnorhynchus sussmilchi.* Dr. Holmes A. Semken, Jr. furnished a number of specimens of *"Dipterus" mordax* and other Upper Devonian fishes from Iowa. Dr. Richard Lund

[1] *Dipnorhynchus lehmanni* should probably be distinguished generically from the type species, *D. sussmilchi,* because of its entirely different dental apparatus and palatal structure.

[2] In the type species of *Ganorhynchus, G. woodwardi,* the palate is not preserved, so the presence or absence of tooth plates cannot be determined.

generously gave Field Museum numerous juvenile dental plates of *Monongahela dunkardensis* from the Permian of Pennsylvania.

MARGINAL TEETH AND JAW BONES

The different types of dental equipment of early Dipnoi were developed for the most part on the pterygoids, vomers[1], and parasphenoid of the palate, and on the prearticulars of the lower jaws. Marginal bones, together with their teeth, were reduced or lost. However, a few Paleozoic genera retain traces of marginal jaw elements and teeth. Small denticles have been found on the dentaries and on the "upper lip" of *Dipterus* (Traquair, 1878, p. 8; Watson and Day, 1916, p. 33; Gross, 1964, p. 11), *Holodipterus* (Gorizdro-Kulczycka, 1950, pp. 89-90) and *Ganorhynchus splendens* (Gross, 1965, p. 131). Small marginal jaw elements, some possibly maxillae, premaxillae and dentaries, others perhaps palatines or ectopterygoids, have been reported in *Dipterus* (Watson and Gill, 1923, pp. 206, 208), *Phaneropleuron* (Watson and Day, 1916, p. 36), *Scaumenacia* and *Uronemus* (Graham-Smith and Westoll, 1937, p. 252; Stensiö, 1947, fig. 32), and *Conchopoma* (Kner, 1868, p. 280; Denison, 1969, p. 200). These are remnants of primitive features, inherited from ancestors in which marginal teeth and jaw elements had not been completely lost.

LUNGFISHES WITHOUT TOOTH PLATES

The variety of dental equipment evolved by early Dipnoi is considerable. The simplest condition is the presence of small denticles, composed of orthodentine, distributed over the palate and prearticulars. This condition is surely the most primitive also since many fishes show the capability of developing denticles on the palate and visceral arches. Ontogenetically, even the complicated dental plates of *Neoceratodus* and *Protopterus* begin to form as isolated denticles. Denticulate pterygoids, parasphenoid and probably prearticulars are well developed in the late Paleozoic *Conchopoma* (fig. 1F), though this genus may be specialized in having some of its palatal teeth opposed by a lower, median denticulated plate supported by the basihyal (Denison, 1969, p. 199). The Upper Devonian *Soederberghia* lacks dental plates and is said to have its pterygoids, anterior part of the parasphenoid, and prearticulars covered with minute denticles, but these have not been adequately figured (Lehman, 1959, pp. 26, 31; pl. 17, fig. B). Better known is the structure in another

[1] Dermopalatines of Schultze (1969, p. 34); anterior pterygoids of Thomson and Campbell (1971, p. 66).

Upper Devonian genus, *Griphognathus,* in which dental plates are also lacking. On the palate, the anterior part of the parasphenoid, the pterygoids, and the vomers are denticulate, and on the lower jaws the same is true of the prearticulars, anterior dentaries, and adsymphysial tooth plate (Schultze, 1969, pp. 22, 33-34; figs. 4, 14-15). In addition, there is a long, median denticulate plate probably supported by the basihyal *(idem,* p. 25; fig. 5). On the dorsal edges of the prearticulars some of the denticles are slightly enlarged and flattened conical in shape, but though tooth-like, they are still extremely small (fig. 1H). The histology of the denticles is simple, consisting of dentine with tubules radiating from slightly branched pulp canals, and covered by relatively thick enameloid (Gross, 1956, pp. 132-133; fig. 124).

There is no direct evidence on the manner of formation or replacement of denticles in these dipnoans. Presumably they form, as in other fishes, in the mucous membrane lining the mouth in places where it covers palatal or mandibular bones. Denticles may be shed as the result of accidents or resorption and replaced perhaps by larger ones. Pits where denticles have probably been shed can be seen in *Conchopoma edesi* (PF 5904, parasphenoid) and *Conchopoma arctata* (PF 6512, lower tooth plate). A broken section of the latter showed no replacement denticles under functional ones; a few depressed denticles may represent replacements, but are more likely older denticles that are being overgrown.

Other genera that retain a denticulate palate and lower jaws have some of the teeth enlarged and specialized in different ways. In the Lower Devonian *Uranolophus wyomingensis* (fig. 1B), on the lateral margins of the pterygoids and on the dorsal margins of the prearticulars and dentaries, instead of enlarged denticles there are continuous "tooth ridges" (Denison, 1968, pp. 382-386; figs. 8, 14-15), which when unworn have an irregular biting edge with many medial projections. The small denticles of *Uranolophus* are composed of simple orthodentine covered by thin enameloid,[1] but on the tooth ridges the enameloid and orthodentine are underlain by trabecular dentine with numerous long, branched pulp canals perpendicular to the surface, and with branched dentine tubules extending out from these canals (Denison, 1968, fig. 23E). There is convincing evidence that the "tooth ridges" were periodically shed or resorbed and replaced as the fish grew. This is indicated by the fact that a small individual (PF 3792) has a small "tooth ridge" that is heavily worn, while a larger individual (PF 3805) has a correspondingly large, almost unworn

[1] The term enameloid is used for the shiny, highly mineralized external coating of certain lungfish teeth, since in no case has the ectodermal origin of this tissue been proven in Dipnoi.

"tooth ridge"; a third individual (PF 3816) lacks "tooth ridges" on the pterygoids.

The Upper Devonian *Holodipterus sanctacrucensis* (fig. 1E) has on the lower jaws, in addition to small denticles on the prearticulars and adsymphysial plate, three pairs of large conical teeth on each prearticular, and a row of small conical teeth on each dentary (Gorizdro-Kulczycka, 1950, pp. 89-90). The large teeth are composed of simple trabecular dentine surrounded by a layer of orthodentine, and were thought by Gorizdro-Kulczycka to be periodically shed and replaced (*idem,* pp. 90, 92). On the palate of *Fleurantia* (Graham-Smith and Westoll, 1937, p. 249) the pterygoids and a bone identified as "? dermopalatine" (possibly a vomer) are denticulate, but the former has also a number of enlarged conical teeth arranged in four radiating rows (fig. 1I), corresponding in position and arrangement to the ridges of a dipnoan tooth plate. At the postero-mesial end of each row are "circles" indicating the position of the bases of larger teeth that have been shed, and within the "circles" are one or more denticles. As interpreted by Bystrow (1944, p. 31), each pterygoid grew in part by additions to its lateral margin, and as it grew, new and larger teeth were added to the antero-lateral ends of each tooth row. At the same time, teeth were shed at the postero-mesial ends of the rows and were not replaced by functional teeth, but merely by denticles.

Three genera that apparently lack denticulation have evolved teeth quite different from the typical dipnoan tooth plates. The Lower Devonian "*Dipnorhynchus*" *lehmanni* (fig. 1A) and the Middle Devonian *Ganorhynchus splendens* (fig. 1C) have one or two rows of elongate, blunt, knob-like teeth on the margins of the pterygoids, and in *Ganorhynchus* at least, also on the "upper lip." The Carboniferous *Uronemus* (fig. 1G) has one or two rows of compressed, sharply pointed teeth on the margins of the pterygoids and prearticulars (Watson and Gill, 1923, p. 200).

One of the earliest known lungfishes, *Dipnorhynchus sussmilchi* (fig. 1D), had evolved a peculiar, unique, and clearly specialized adaptation for crushing food, probably hard food. This consists of rather formless elevations of the palate and lower jaw, formed of thickened trabecular dentine resting directly on the underlying bone (White, 1966, p. 7). There is no evidence to indicate how this dentine formed, or whether it continued to grow next to or into the spongy bone at its base as the buccal surface became worn.

LUNGFISHES WITH TOOTH PLATES

All the other dipnoan genera in which the dental apparatus is known have tooth plates formed of radiating rows of teeth or of radiating

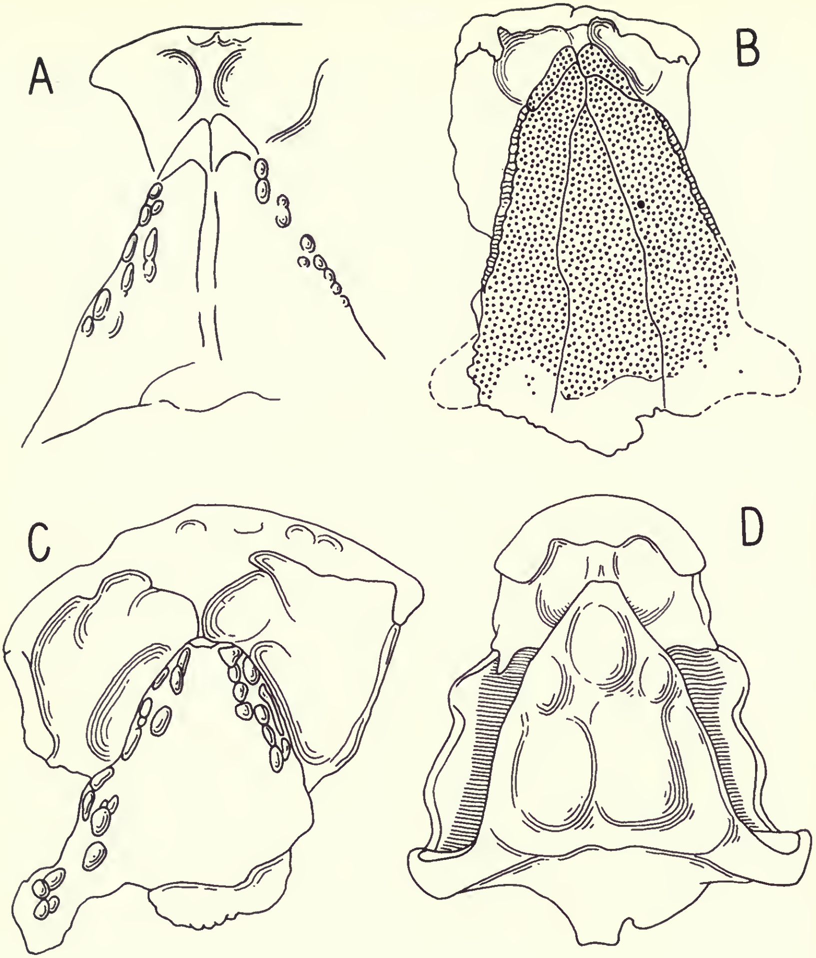
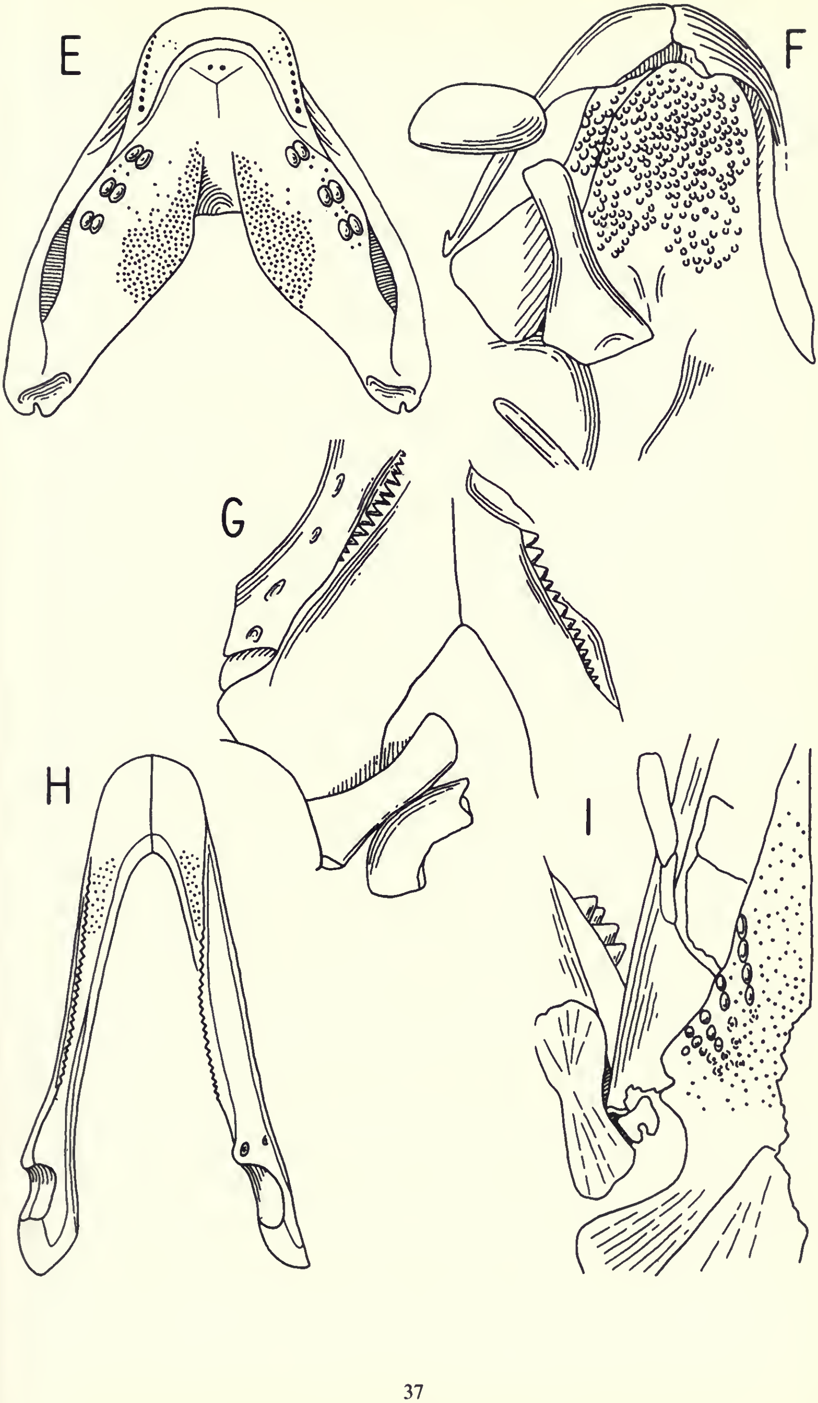


FIG. 1. Dental apparatuses of lungfishes without tooth plates, redrawn at various scales. **A,** *"Dipnorhynchus" lehmanni,* palate, after Lehmann and Westoll, 1952, and Jarvik, 1954; **B,** *Uranolophus wyomingensis,* palate, after Denison, 1968; **C,** *Ganorhynchus splendens,* palate, after Gross, 1965; **D,** *Dipnorhynchus sussmilchi,* palate, after Thomson and Campbell, 1971; **E,** *Holodipterus sanctacrucensis,* lower jaws, after Gorizdro-Kulczycka, 1950; **F,** *Conchopoma gadiformis* and, **G,** *Uronemus splendens,* palates, after Watson and Gill, 1923; **H,** *Griphognathus minutidens,* lower jaws, after Gross, 1956; **I,** *Fleurantia denticulata,* palate, after Graham-Smith and Westoll, 1937.


E
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ridges attached to the pterygoids and prearticulars; small vomers anterior to the pterygoids may bear teeth also. The origin, evolution, and ontogeny of these tooth plates are of considerable interest, but are not adequately known. The wide variety of dental apparatuses in Devonian Dipnoi is evidence of early experimentation, but does not give any conclusive proof of what is the primitive condition. White (1965, p. 39; 1966, p. 7) and Thomson (1967, p. 5) believed that a thick layer of dentine, such as occurs in *Dipnorhynchus sussmilchi,* was primitive, and that a denticulated tooth plate, such as occurs in *Dipterus,* was derived from it. The uniqueness of the *Dipnorhynchus sussmilchi* condition indicates that it was more probably specialized, in spite of its Lower or Middle Devonian age. A more probable ancestral condition is denticulation of parts of the palate and lower jaws, such as occurs in a number of the early dipnoans discussed above. The *Fleurantia* condition, in which some of the denticulations have become enlarged and arranged in radiating rows resembling the pattern of tooth plates, could be converted simply to tooth plates if the individual denticles became firmly attached to the underlying bone, and instead of being shed, continued to grow by addition of new dentine at their bases to keep pace with wear at their crowns.

Starting with some such primitive condition, the evolution of lungfish tooth plates involves a number of factors. One has to do with the acquisition of a variety of shapes and surface forms adapted to chewing different foods; this will not be discussed in this paper. Another concerns the mechanisms by which a tooth plate maintains itself as its surface is worn down by chewing. A third has to do with the evolution of specialized tissues that resist wear and produce a functional biting surface. Some aspects of the tissue evolution will be considered first.

The small denticles that cover parts of the palate and lower jaws of *Uranolophus* consist of orthodentine and the same is true of the isolated denticles that first appear in the ontogeny of the tooth plates of *Neoceratodus* and *Protopterus.* As tooth plates become larger, the denticulations that form the crests of their ridges also become larger, and no longer have such a simple histology. The unworn denticulations of an adult tooth plate of *Dipterus valenciennesi* or *Scaumenacia* have a thin surface layer of orthodentine covered by enameloid, but the body of the tooth is composed of a mass of trabecular dentine in which the vascular or pulp canals are somewhat irregular, branch, and anastomize occasionally with one another. Formation of such trabecular dentine is not restricted to lungfishes, for it develops in a similar way in larger teeth of many elasmobranchs and bony fishes, and is surely related to the problem of forming relatively sizeable masses of dentine at some distance from the

surface of the tooth. In many post-Devonian lungfish tooth plates, this primitive type of trabecular dentine has been modified into a specialized variety known as tubular dentine, in which the vascular or pulp canals are nearly parallel to each other and perpendicular to the surface of the tooth. The dentine tubules in these trabecular dentines extend from the pulp canals usually more or less obliquely to the side and toward the surface of the tooth, and may have many fine branches.

A feature of the simple trabecular and tubular dentines of lungfish tooth plates is that they are highly mineralized, which, of course, makes them harder than ordinary dentines and more resistant to wear. This condition is indicated in fossil lungfish tooth plates not only by the resistance, but also by the fact that the dentine is usually clear and transparent, presumably because it is so dense that it cannot easily be penetrated by natural stains. The term "pleromic" has been applied by Ørvig (1967, p. 89) to these and to other tissues characterized by their hardness due to hypermineralization, but this usage is inappropriate; it was originally applied to a secondary dentine that fills vascular spaces in worn spongy bone of Heterostraci (Tarlo and Tarlo, 1961, p. 161), and the term pleromic itself is derived from a Greek word meaning "that which fills." A secondary pleromic dentine in the original and restricted sense does occur in lungfishes, as will be shown below, but the name will not be used here for the typical trabecular or tubular dentine of dipnoan dental plates.

It is well known that in most dipnoan tooth plates the dentine continues to grow at its base to keep up with wear on the crown. Some of the earliest lungfishes had not yet evolved a mechanism that accomplished this with complete success. This is the case in *Dipterus valenciennesi,* a Middle Devonian lungfish which is primitive in that the radiating ridges of its tooth plates are composed typically of individual denticles, each more or less completely separate from its neighbor. Each denticle, when unworn, is composed of enameloid and orthodentine surrounding a core of trabecular dentine with branched, more or less vertical pulp canals from which arise the dentine tubules. The dentine is attached directly to the underlying bone with no intervening pulp chambers separating the two tissues. An important difference from *Fleurantia* is that there is almost surely no shedding and replacement of the denticles; Bystrow's (1942, p. 280) description of the shedding by resorption of individual denticles in *Dipterus* has not been confirmed. It is also certain that the tooth plates themselves were not shed and replaced; Rosë's (1892, p. 837) suggestion that this happened in *Protopterus* during aestivation is certainly incorrect. The tooth plates of *Dipterus* grew in area, as the fish grew, essentially by adding new and usually larger denticles at the anterior and

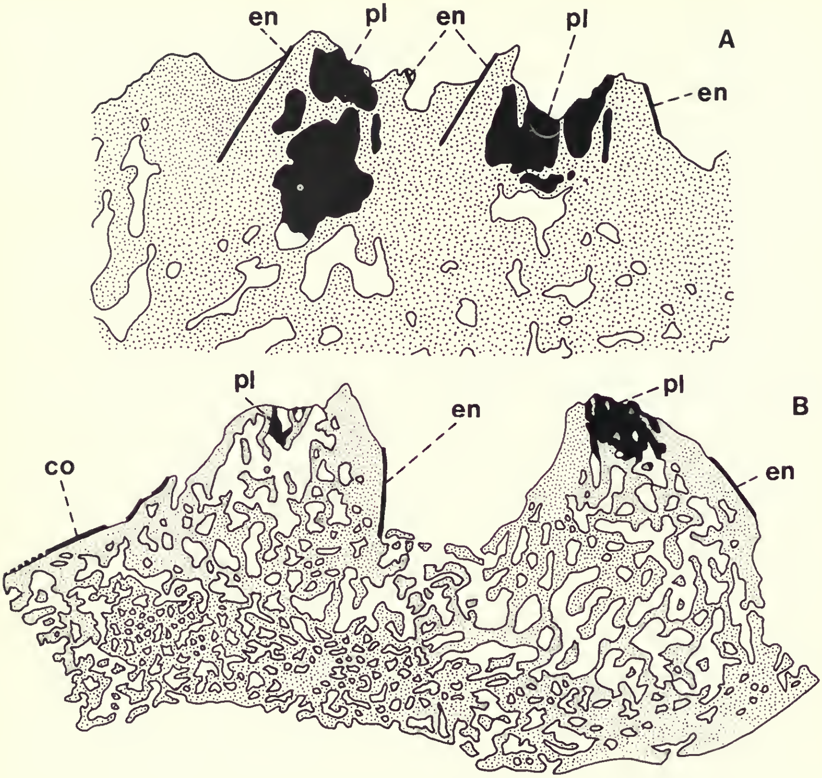


FIG. 2. *Dipterus valenciennesi* Sedgwick and Murchison, sections through tooth plates. **A,** lower tooth plate, Royal Scottish Museum 1859.33.647, (×48); **B,** upper tooth plate, Royal Scottish Museum 1957.1.690, (×25). *co,* cosmine; *en,* enameloid; *pl,* pleromic dentine.

lateral ends of the tooth rows or ridges. *D. valenciennesi,* however, had not evolved a completely successful means of increasing the thickness of the tooth plate, or of keeping up with the surface wear on the crown. As the crowns of the denticles were worn away, repair was made by filling the canals of the trabecular dentine and the cavities of the underlying spongy bone with a very dense calcification (fig. 2, *pl*), which is a pleromic dentine in the strict sense, as proposed in 1961 by Tarlo and Tarlo. Pleromic dentine is also sometimes seen filling cavities of spongy bone between rows of denticles. The deposition of this hard tissue was an effort to repair the denticles as they were worn, but was not always successful, inasmuch as the denticles sometimes completely disappeared near the postero-median parts of the tooth plates, leaving only a rough bone surface partially filled with pleromic dentine. In the latter case, it is assumed that the formation of pleromic dentine was not rapid enough to keep up

FIG. 3. *Dipterus fleischeri* (Newberry), upper dental plate, New York State Museum 10341, (x2).

with the rate of wear, but in some individuals and species it is, and then the pleromic dentine, because of its superior hardness, forms elevated cusps. This is beautifully shown in a tooth plate of *Dipterus fleischeri* (fig. 3) in which the cusps are formed by black pleromic dentine contrasting sharply with the whitish trabecular dentine in which it was formed and by which it is surrounded.

Another peculiar feature of the tooth plates of *Dipterus valenciennesi,* which in some cases may be related to wear on their older parts, is the formation of a layer of cosmine along the medial margins of the plates. White (1965, p. 39; 1966, p. 7) apparently thought this cosmine was a primitive feature, and considered its irregular medial margins to be the result of resorption. Jarvik (1967, p. 166) believed this dental cosmine may have been periodically resorbed and reformed, as is the case with the cosmine on the skull roof. In the specimens available to me, the margins of the cosmine, though irregular in outline, are rounded off toward the underlying bone surface, and so are clearly margins of formation, not resorption. In some tooth plates (Royal Scottish Museum 1859.33.615) there is a single area of cosmine, but in others there are several contiguous areas or generations separated by Westoll lines. Thus in Field Museum

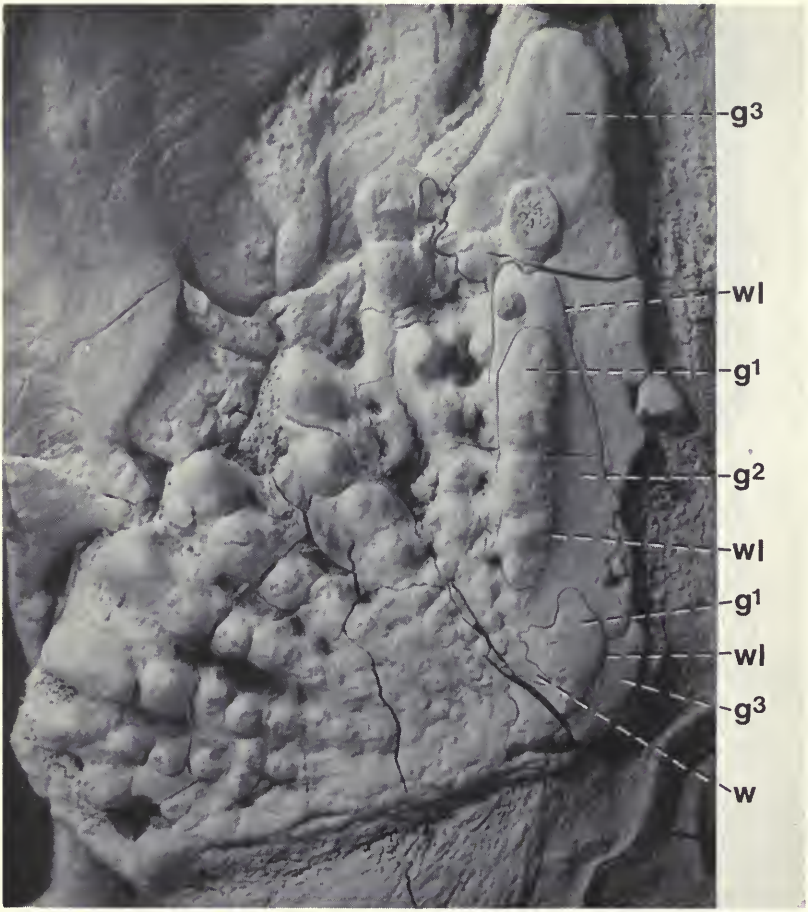
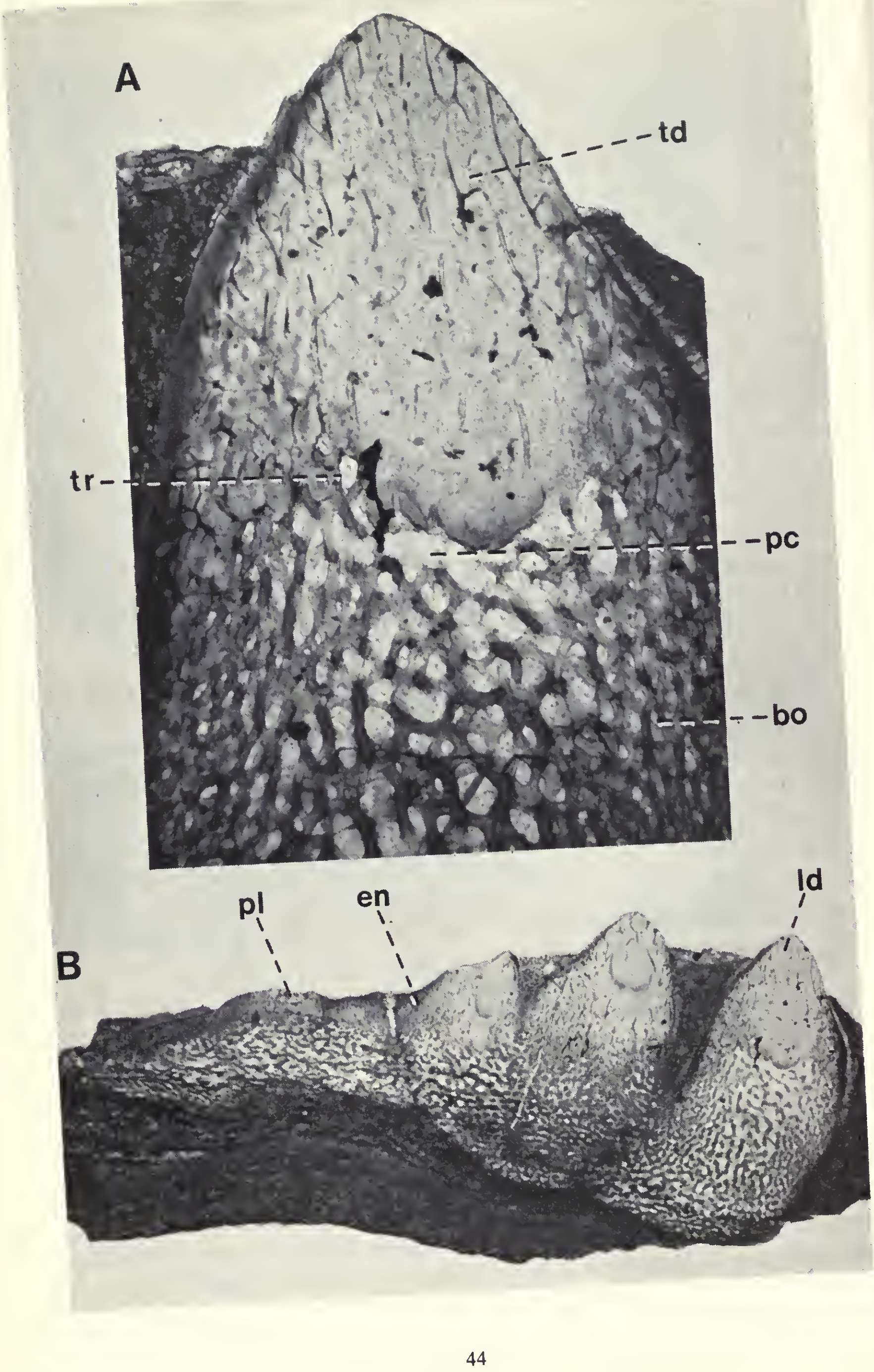


FIG. 4. *Dipterus valenciennesi* Sedgwick and Murchison, right upper tooth plate, Field Museum PF 1293, (×7). g^1, g^2, g^3, first, second, and the third generations of cosmine; *w*, worn area in cosmine; *wl*, Westoll lines, retouched for emphasis.

PF1293 there are five areas of cosmine, representing at least three generations, which have been identified on Figure 4. The first generation (fig. 4, g^1) nearly covers four denticles near the center of the medial row; it is also possibly represented by a small patch near the postero-medial corner of the tooth plate in which there is a worn area. The second generation (fig. 4, g^2) bounds a short segment of the medial edge and surrounds one denticle of the medial row; it shows a probable area of wear posteriorly. The third generation (fig. 4, g^3) bounds some of the anterior and most of the median edge of the tooth plate and surrounds a large denticle anteriorly; it shows no evidence of wear; a small patch at the postero-

medial corner of the tooth plate may belong to this generation. The three generations presumably formed at three successive stages of growth, perhaps corresponding to the periods of cosmine formation on the skull roof and jaws. An undescribed dipnoan tooth plate from Antarctica shows beautifully five generations of cosmine, which form parallel bands along the medial margin and the medial row of denticles. Each successive generation is clearly related to more anterior denticles of the medial row.

Tooth plates referred to *Dipterus verneuillii* and *D. tuberculatus* by Pander (1858, pl. 5) appear to differ from *D. valenciennesi* in having a somewhat greater development of trabecular dentine in the denticles, and in the presence of a small pulp chamber between the dentine and the underlying spongy bone. Very similar histologically are the tooth plates of *Scaumenacia curta*. In this species the denticles are separated from each other, are imbedded in spongy bone, and, in fact, have their bases composed of spongy bone. A thin layer of enameloid presumably covered their surface, but this is worn off the tips of the denticles, and in slide 5158 (fig. 5B, *en*) is preserved only around the imbedded bases of some denticles. Underlying this is a thin layer of orthodentine, but the body of the denticle is composed of a transparent, highly mineralized, trabecular dentine, penetrated by branching pulp canals directed towards the tip or obliquely towards the side of the denticle (fig. 5A, *td*). Where the surface of the denticle is preserved, the pulp canals terminate in clusters of dentine tubules which form the superficial layer of orthodentine; thus the canals of the trabecular dentine are in part direct continuations of the pulp chambers of the orthodentine. Where the surface is worn and the orthodentine removed, the pulp canals open onto the surface. The dense trabecular dentine clearly grew at its base. In slide 5158 the largest and last formed denticle, though not the others, has a small pulp cavity at the base of the central part of the trabecular dentine (fig. 5A, *pc*), and this was formed by resorption of the underlying bone. However, resorption was not complete in advance of the growing dentine because an occasional bone trabecle (fig. 5A, *tr*) is enclosed in the central part of the trabecular dentine, and at the sides of the denticle little bone has been removed and dentine fills the cavities of the spongy bone. That dentine which fills cavities in bone may be considered pleromic in the sense of Tarlo and Tarlo (1961), but the mass of the denticle is ordinary trabecular dentine. The most proximal denticle in slide 5158 has been completely removed and is indicated only by a small patch of pleromic dentine in the bone (fig. 5B, *pl*). This suggests that, as in *Dipterus valanciennesi, Scaumenacia* had not yet evolved an efficient mechanism for keeping up with wear on the tooth surface.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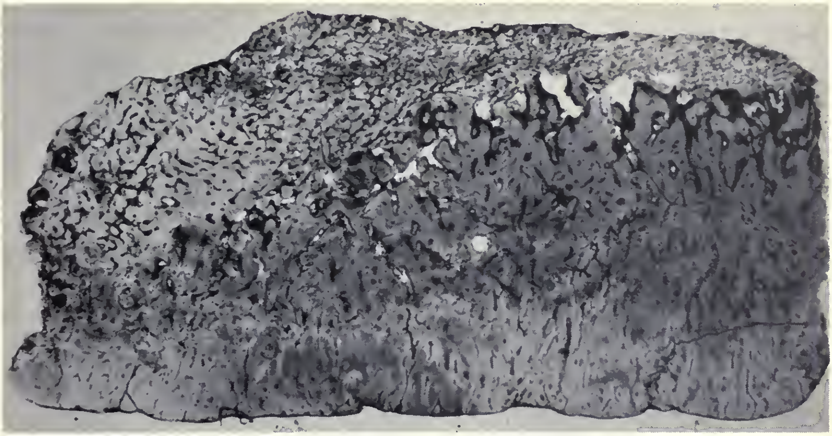

FIG. 6. *"Dipterus" mordax* Eastman, vertical section through row of worn denticles on tooth plate, Field Museum slide 5509, (x12).

A large number of species of *Dipterus* have been based on tooth plates alone, and it is probable that if these species were more completely known, many would be removed to different genera. Such a one is *"Dipterus" mordax* Eastman from the Upper Devonian of Iowa, which is characterized by having six rows of large, rounded denticles. These denticles are quite discrete when little worn, but those in one row tend to form a smooth, punctate, uniform ridge when much worn, and those in the oldest postero-medial part of the tooth plate tend to wear to a continuous, smooth, punctate area. The reason for this is clear when the histology is examined in thin sections (fig. 6), which show that the denticles do not differ from the intervening tissue, and that both are composed of trabecular dentine. This trabecular dentine is thick, but is unspecialized in having its pulp canals somewhat irregular, branching, and anastomizing. Below its growing base are small pulp chambers formed by resorption of the underlying spongy bone. The formation and growth of these teeth is presumably similar to that of *Sagenodus.*

Tooth plates of *Sagenodus* show considerable advance over the condition of *Dipterus valenciennesi* and *Scaumenacia,* and some advance over that of *"Dipterus" mordax.* Sections of a tooth plate of *Sagenodus* sp. (fig. 7) reveal that its crown is composed of a thick layer of highly mineralized tubular dentine (fig. 7, *tu*) in which the pulp canals are quite reg-

FIG. 5. *Scaumenacia curta* (Whiteaves), Field Museum slide 5158. **A,** vertical section through most lateral cusp of row of denticles, (x43); **B,** vertical section through entire row of denticles, (x11). *bo,* bone; *en,* enameloid; *ld,* lateral denticle figured in A; *pc,* pulp cavity; *pl,* pleromic dentine; *td,* trabecular dentine; *tr,* bony trabecle imbedded in dentine.

ular, perpendicular to the surface, and have few branches or anastomoses. This is attached to the underlying spongy bone at the ends and sides of the tooth plate, but elsewhere is separated by a widely open pulp chamber (fig. 7, *pc*) that is formed presumably by resorption of the bone surface

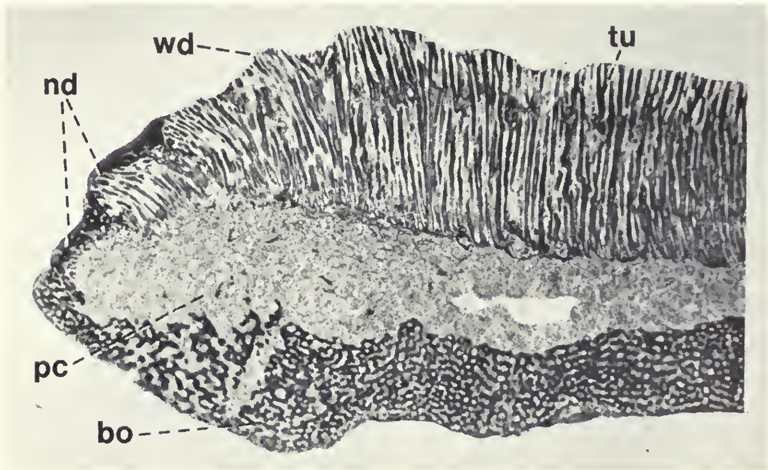

FIG. 7. *Sagenodus* sp., vertical section of a tooth plate through a ridge crowned with worn denticles, Field Museum slide 4261, (x8). *bo*, bone; *nd*, latest denticles to have formed; *pc*, pulp chamber; *tu*, tubular dentine; *wd*, worn denticles.

well in advance of the growing lower surface of the tubular dentine. Worn surfaces of the tooth are formed by the tubular dentine, and appear to be punctate due to the terminations of the pulp canals. At the anterior and lateral ends of the ridges, the tooth plate grows by addition of new denticles, and where unworn, they reveal the manner in which they were formed. Under a thin superficial enameloid, there is a thin orthodentine passing into a layer of spongy trabecular dentine, both brown stained. The latter passes abruptly into tubular dentine which is distinct not only because of its relatively straight, parallel canals, but also because it is clear, unstained, and highly mineralized. In a newly formed denticle (fig. 7, *nd*) the tubular dentine is thin and its canals are horizontal and thus nearly at right angles to the canals in the older part of the tooth plate. As such a denticle grows by addition of more tubular dentine to its base, the canals curve to assume a direction more nearly parallel to those in the older part of the tooth plate. In other tooth plates of *Sagenodus* sp. (slides 5159-60, 5508) there is no development of trabecular dentine between the orthodentine and tubular dentine.

Tooth plates of the Ceratodontidae, including the Recent *Neoceratodus* and its Mesozoic and Cenozoic allies, could be derived without funda-

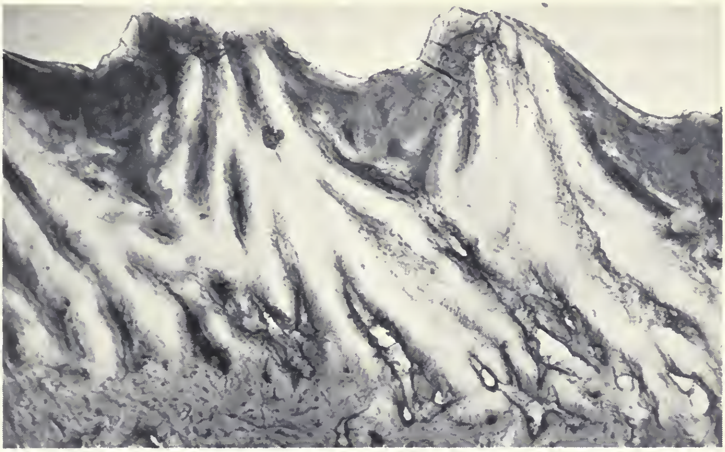

FIG. 8. *Ceratodus parvus* Agassiz, vertical section through two denticles of a juvenile tooth plate, Field Museum slide 4846, (×40).

mental alterations from those of *Sagenodus,* but due to the fact that only the earliest stages of the development of *Neoceratodus* tooth plates are known, there has been considerable uncertainty about how the complicated adult tooth plates are formed. In the most advanced stage studied by Semon (1901, pl. 19, fig. 11) the tooth plates are represented by rows of minute separate tooth anlagen, each composed of a cone of orthodentine. Presumably these anlagen later attached to the underlying bone, and they may have grown at their bases, but it is quite certain that these original orthodentine cones and their pulp cavities never gave rise to columns of tubular dentine and pulp canals. The tissue of embryonic *Neoceratodus* is simple because of the small size of its denticles. Tooth plates of juvenile *Ceratodus parvus* from the Rhaetic described by Peyer (1959, p. 152, fig. 6) are larger and more complicated in structure. They have individual denticles on the ridges, but these are fused at their bases. The denticles, when unworn (fig. 8), have a coating of enameloid, a layer of orthodentine, then a core of highly mineralized trabecular dentine; the latter is unspecialized, and is not separated from the underlying bone by an open pulp chamber. The larger adult tooth plates of *Neoceratodus forsteri* (fig. 9) are quite different. The ridges are, of course, worn and show no sign of individual denticles. The body of the plate is made up of well organized tubular dentine, separated from the underlying bone by a widely open pulp chamber. The growth in thickness of the dentine was just as in *Sagenodus,* but the manner of areal growth is not obvious because of the absence of any well-marked, newly formed denticles at the

distal ends of the ridges. However, the lateral margin of each of the ridges of the pterygoid tooth plates of Field Museum 59936 shows two or three small, shiny convexities that appear to indicate additions to the ridges.

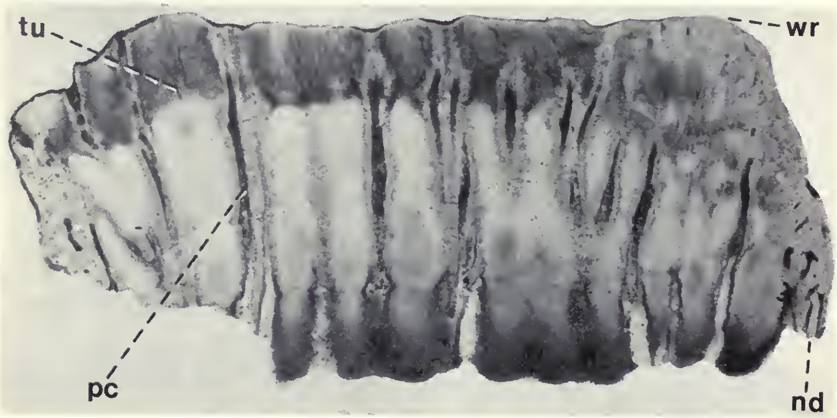

FIG. 9. *Neoceratodus forsteri* Krefft, vertical section through posterior ridge of left upper tooth plate, lacking bony base, Field Museum slide 5513, (x18). *nd*, new dentine at distal end of ridge; *pc*, pulp canal; *tu*, tubular dentine; *wr*, worn surface of ridge.

In thin section (slide 5513, fig. 10) these convexities are seen to be composed of enameloid-coated dentine whose tubules extend mostly laterally from a number of small pulp canals (fig. 10, *pc*). The latter join basally to form a larger vertically directed pulp canal, comparable to and parallel to the adjacent canals of the tubular dentine. It appears then that each of the lateral convexities on the tooth plate ridges forms basally a new column of tubular dentine, and thus enlarges the tooth plate laterally.

The early stages of growth of the tooth plates of the specialized Recent lungfish, *Protopterus aethiopicus,* have been described by Lison (1941, 1954, pp. 814-815). The first anlagen of the tooth plates are isolated denticles formed of ordinary orthodentine. At a certain depth each denticle starts forming at its base a very dense, whitish, highly mineralized tissue, called petrodentine by Lison. This continues to grow basally so that below each original denticle there is formed a column of very dense tissue that persists in the adult tooth. Between these dense columns there appears in some manner a tube that becomes surrounded by layers of less dense, yellowish, trabecular dentine, called "pseudohaversian osteodentine" by Lison. In a worn tooth, the surface is composed of small areas of denser petrodentine surrounded by softer trabecular dentine, and wear produces a rough, resistant surface.

Ground thin-sections of adult *Protopterus dolloi* tooth plates (fig. 11A) are helpful in understanding some details of their manner of growth. Dentine tubules extend obliquely toward the petrodentine columns from

FIG. 10. *Neoceratodus forsteri* Krefft, vertical section through distal end of ridge shown in Figure 9, Field Museum slide 5513, (x55), *nd*, new dentine; *pc*, pulp canals.

the canals of the trabecular dentine, and at or near the boundary of these two tissue they break up into numerous very fine branches that penetrate into the petrodentine. At the bases of the petrodentine columns, most or all of the tubules are directed obliquely towards the sides of the columns (fig. 11B) and must have terminated in odontoblasts that were lateral to the petrodentine. This suggests that, though the hypermineralization may have proceeded directly down the columns, the growth of the columns was obliquely from the sides, and indicates that the trabecular dentine and most or all of the petrodentine were formed by the same odontoblasts. This manner of growth would explain in *Protopterus aethiopicus* the penetration of the petrodentine by fine branches of the dentine tubules arising

in the canals of the "pseudohaversian osteodentine" (Lison, 1941, p. 293, fig. 4). It should also be noted that in available sections of *P. dolloi* the

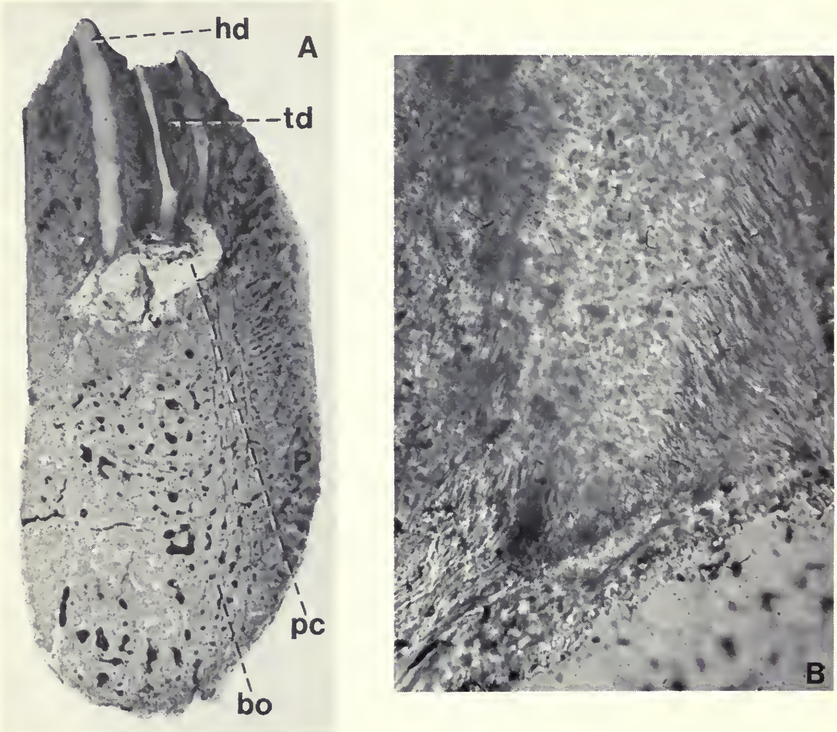

FIG. 11. *Protopterus dolloi* Boulenger, vertical transverse section through middle ridge of right lower tooth plate, Field Museum slide 5514. **A,** entire section, (x14); **B,** base of left petrodentine column shown in A, (x135). *bo,* bony base; *hd,* hypermineralized dentine or petrodentine; *pc,* pulp chamber; *td,* trabecular dentine between petrodentine.

lamellar, "pseudohaversian" structure of the trabecular dentine, described by Lison in *P. aethiopicus,* is not apparent.

Very small dental plates of *Monongahela dunkardensis* from the Permian Greene formation of western Pennsylvania are of considerable interest not only because they represent an early developmental stage, but also because they show a very distinctive histological structure that is comparable in some respects to that of *Protopterus.* In thin-section, unworn denticles are capped by thin enameloid (fig. 12B, *en*), beneath which is a very thin layer presumably of orthodentine. This is underlain by a column of what appears to be a dense, highly mineralized tissue,

sometimes clear, but often stained gray (fig. 12, *hd*). Pulp chambers are not apparent under these columns of dense tissue, but rather between them, and from these chambers extend relatively large dentine tubules mostly obliquely towards the crowns of the denticles and the underlying columns of dense tissue; a few tubules rise from the pulp cavities directly towards the surface between the denticles. The tubules give off many fine branches, but where they reach the column of dense tissue they break up into tufts of very fine tubules that extend into its center, where they form a dense, irregular network (fig. 13). Larger specimens are not available to me, but it seems probable that later in development these tooth plates could approach *Protopterus* in structure, with the dense, highly mineralized tissue becoming "petrodentine" columns, and the intervening pulp chambers producing a softer trabecular dentine surrounding the columns. In any case, it is possible that the *Protopterus* histology could have evolved from that shown by these juvenile Permian tooth plates. The evident migration of the pulp chambers from their presumed original position beneath the enameloid crowns to a position between the crowns suggests a means by which the tubes at the center of the "pseudohaversian osteodentine" columns of *Protopterus aethiopicus* might have originated. This was not shown in the material available to Lison (1941, p. 309), who suggested two possible origins for the tubes: that they were formed by resorption; or that they resulted from localized absence of growth of the roof of the pulp chamber.

The Recent South American *Lepidosiren* has tooth plates comparable to those of *Protopterus* in being constructed partly of columns of highly mineralized dentine separated by less dense trabecular dentine (fig. 14). However, the crests of the three radiating ridges on each tooth plate are formed by a thick band of very hard dentine, apparently formed on the anterior and antero-lateral faces of the ridges as ordinary orthodentine, then hypermineralized. Near its base, this dentine is bounded internally by the large pulp chamber, but near the crest it passes inwards into trabecular dentine interspersed with columns or projections of highly mineralized dentine.

The late Paleozoic *Gnathorhiza* has been considered a relative of *Protopterus* and *Lepidosiren* largely because of the form of its tooth plates (Romer and Smith, 1934, pp. 717-718; Carlson, 1968, pp. 653-654; Lund, 1970, pp. 254-255). However, thin-sections of *G. dikeloda* (slide 5162) and of *G. serrata* (fig. 15) show no indication of alternating columns of petrodentine and trabecular dentine; rather, the crests of the ridges are formed of ordinary trabecular dentine.

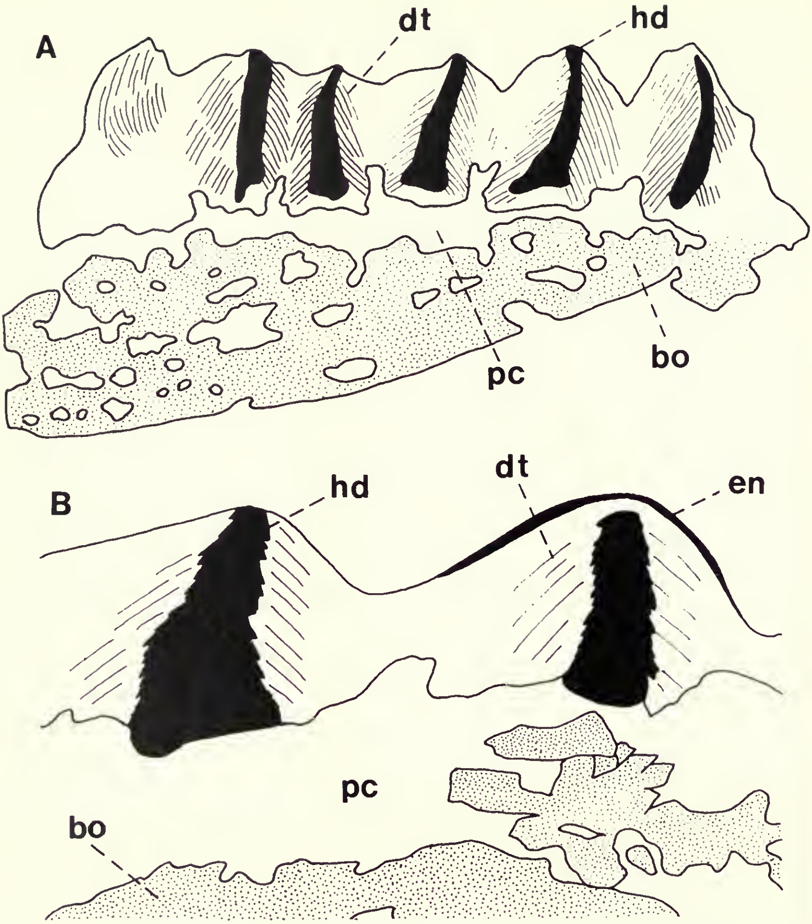

FIG. 12. *Monongahela dunkardensis* Lund, juvenile dental plates. **A,** vertical longitudinal section through entire tooth ridge, Field Museum slide 5502, (×100); **B,** vertical section through two denticles, Field Museum slide 5507, (×200). *bo,* bony base of tooth plate, partly crushed into pulp chamber in B; *dt,* dentine tubules; *en,* enameloid; *hd,* columns of hypermineralized dentine; the base of the right column in B not determinable; *pc,* pulp chamber.

In the paragraphs above, discussion of the growth of the tooth plates of *Protopterus* and *Lepidosiren* has been limited to their increase in thickness. As the fishes grew, there was certainly also areal growth of the tooth plates to match the increasing size. This was clearly not accomplished by the addition of new cusps or denticles to the distal ends of the ridges, as in *Sagenodus.* No such denticles are apparent on specimens available to me, and moreover, both the medial and lateral vertical

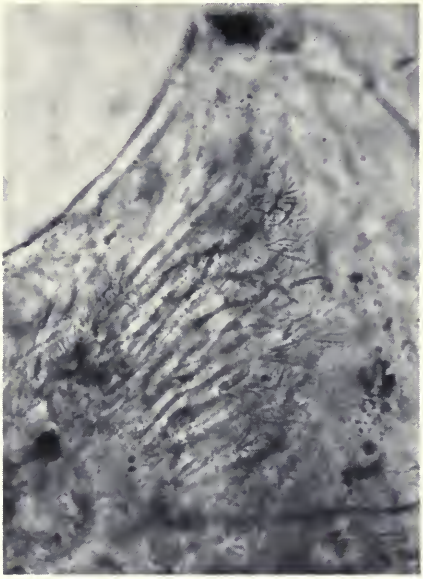

FIG. 13. *Monongahela dunkardensis* Lund, vertical section through denticle of juvenile tooth plate, showing terminal branching of dentine tubules; Field Museum slide 5505 (x385).

faces of the tooth ridges are coated with enameloid showing distinct growth lines. The areal growth appears to have been accomplished simply by an increase in the dimensions of the dentine at its growing base; thus, as the narrow crest wears down, the ridges become wider and longer.

PHYLOGENETIC CONCLUSIONS

Recently Thomson and Campbell (1971, p. 100) have questioned the phylogenetic significance of lungfish teeth because they are so clearly adaptations to special manners of feeding. The teeth are adaptive, of course, but surely this is true also of the pattern of the skull roof and the form of the parasphenoid to which they give great phylogenetic weight. Similar dental apparatuses or skull roof patterns may possibly have evolved separately and convergently in different phyletic lines, so in our present state of knowledge a single character cannot be accepted as proof of phyletic relationship. However, because they are so complex, it is very unlikely that dipnoan tooth plates have given rise to the simpler dental apparatuses of other lungfishes.

If this is the case, it is clear that during the Devonian, and to a lesser extent during the later Paleozoic, there were a number of distinct phy-

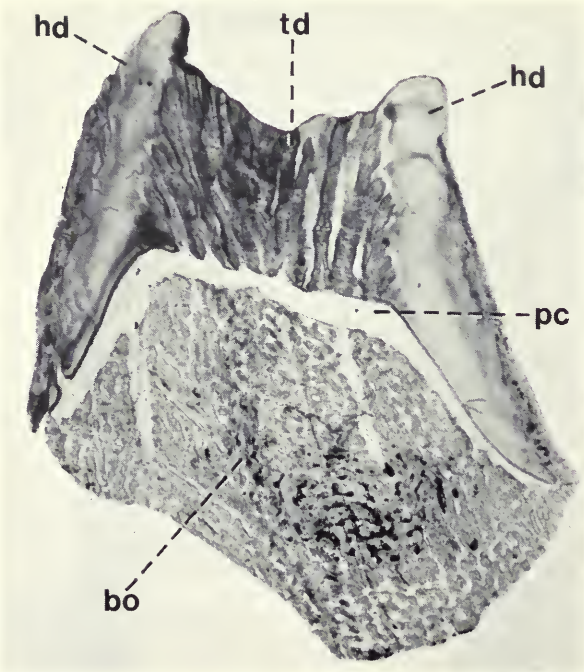

FIG. 14. *Lepidosiren,* vertical transverse section through middle and posterior blades of left lower tooth plate, Field Museum slide 5517, (×10). *bo,* bony base; *hd,* thick bands of highly mineralized dentine; *pc,* pulp chamber; *td,* trabecular dentine and columns of highly mineralized dentine.

letic lines which, at least as far as their dental apparatus is concerned, can be considered as experiments in feeding adaptation. Some retained a denticulation of the palate and lower jaws, a condition I believe to be primitive. Where this is associated with a long snout and jaws (*Soederberghia, Griphognathus,* and *Fleurantia*), it is a weak apparatus, suitable mainly for holding, or perhaps chewing soft food, but not for crushing. However, the shorter-skulled *Conchopoma* with its relatively larger denticles may have crushed plants and soft-shelled invertebrates. Since the denticulation is a primitive character, it is not to be considered by itself as a proof of close relationship; other characters indicate that *Conchopoma* is far removed from the long-snouted dipnoans, and *Fleurantia* has been shown to be unrelated to *Soederberghia* and *Griphognathus* by Schultze (1969, pp. 46-47). Three Lower Devonian dipnoans show great similarity in cranial roof pattern, yet have entirely different dental apparatuses; in this case, the cranial pattern is presumably a primitive feature retained by all three, while their teeth were specialized and

FIG. 15. *Gnathorhiza serrata* Cope, vertical section through ridge on tooth plate showing trabecular dentine and pulp chamber at base; Field Museum slide 4269, (×24).

adapted for different types of feeding. Most primitive is *Uranolophus,* which retains the original denticulation, but has modified it on the edges of the palate and lower jaws into a tooth ridge suitable for chewing or cutting. At the other extreme is *Dipnorhynchus sussmilchi* with its powerful, bulbous, crushing surfaces on the palate and lower jaws. Finally, "*Dipnorhynchus*" *lehmanni* had knob-like teeth on its palate which could have served for chewing or crushing; the Middle Devonian *Ganorhynchus splendens* had similar teeth. The Upper Devonian *Holodipterus sanctacrucensis* had denticulate lower jaws set with a few larger, blunt teeth; the massiveness of the jaws suggests that this was a food crusher. The margins of the lower jaws and pterygoids of *Uronemus* had sharp, compressed-conical teeth which must have served for slicing food.

Dipnoan dental plates probably evolved from the scattered denticles of an ancestor by the enlargement of some and their arrangement in rows. *Fleurantia* illustrates a possible ancestral condition, but this genus is too

late and too specialized in other respects to be ancestral to *Dipterus* or to many other dipnoans with dental plates, and suggests the possibility that tooth plates may have arisen more than once within the group. In the ancestral form, individual denticles could be shed and replaced, but in tooth plates the denticles remained attached to the underlying bone, and grew at their bases into the bone or into a space formed by its resorption. In early lungfishes this growth did not always keep up with wear, and the denticles were sometimes completely removed. The material of the denticles or ridges, at first a simple trabecular dentine, later evolved into a specialized tubular dentine, and was characteristically highly mineralized and resistant to wear. The originally separate denticles became confluent, and wore to continuous ridges or surfaces of trabecular dentine. A large pulp chamber was formed by the resorption of the underlying bone, making it easy for the dentine to grow and thicken at its base as it wore down at the crown. In most genera the tooth plates enlarged by the addition of new denticles of trabecular or tubular dentine at the distal ends of the ridges. One of the modifications that led to the origin of a new family, the Lepidosirenidae, was the formation in the tooth plates of columns of very hard dentine ("petrodentine") surrounded by softer trabecular dentine, a condition foreshadowed by juvenile tooth plates of *Monongahela.* According to Lund (1970, p. 257), the latter shows resemblances to young *Sagenodus,* and may have been derived from a similar form. The late Paleozoic *Gnathorhiza* has been considered to be related to and ancestral to the Lepidosirenidae, but the histology of the tooth plates does not support this.

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